

arcticus, Black-throated Diver, was ascertained to breed in North Uist. I did not however find the nest of the latter bird, but mention the fact upon the authority of several of my friends who did so and know the species well—among others, Lieut. Macdonald of North Uist. The Guillemot, *Uria Troile*, was observed with the Razor-bill in vast numbers in the end of April, while crossing the Minch in the Uist packet, and that too during the whole extent, or about thirty miles. *Uria Grylle*, Black Guillemot, was found on all the rocky coasts, but was nowhere very numerous. The first young bird fully fledged was shot on the 14th of August. Of the Puffin, *Mormon arcticus*, I saw countless myriads in St. Kilda*, where they far outnumber all the other species. *Alca Torda*, the Razor-bill, is also very plentiful in St. Kilda, and, with the Puffin, breeds also in Haskir, but in far smaller numbers. When in St. Kilda I was told by some of the fowlers, that the Great Auk, *Alca impennis*, is still seen occasionally, but that none had been procured for many years back.

IV.—*Researches on the Structure of Annular Vessels.*

By HUGO MOHL†.

[With a Plate.]

DR. SCHLEIDEN lately published some observations on the spiral formations in the cells of plants in the 'Flora' (see *Annals and Mag. of Nat. Hist.*, vol. vi. p. 35), which interested me the more by reason of my having recently directed attention to the same subject (*Flora*, 1839, pp. 81–142), and especially as the result of his researches coincided with my own in all essential points concerning the structure of the cellular membrane of vegetables. His opinion principally differs from mine in two points, viz. the order of development of the secondary membranes and fibres in the woody fibre of *Taxus* and allied organisms, and the formation of the annular vessels.

I must wait for a more favourable opportunity to examine the first point; but, as regards the second, I will state the reasons which induce me to adhere to my former opinion, notwithstanding Schleiden has set forth a new theory respecting the development of the annular vessels.

Long ago (see 'Flora,' 1838, p. 378,) have I been opposed to the hypothesis, which is devoid of all foundation, although generally received even in the present day, that annular vessels owe their origin to the disruption of the spiral fibres of spiral vessels whose fragments become afterwards united in the form

* Where I procured a nearly white variety of this species.

† From the *Flora*, 1839, p. 673.

of rings. On the contrary, I have explained the formation of annular fibres as a mere modification of spiral fibres, founded upon the fact, that the ascension of a spiral fibre, which can, on the one hand, be extended so far as to take a longitudinal direction, may, on the other hand, be diminished to such a degree that its direction may transversely cross the longitudinal axis of the vessel; the consequence of which must necessarily be, rings returning into themselves instead of spiral fibres. On the contrary, Dr. Schleiden thinks that, in the secondary membranes of the utricles of plants, we can, without any exception, demonstrate a spiral disposition of the fibres; and that annular vessels are formed by spiral vessels which have a constant tendency to unroll themselves, the coils of whose fibre become united here and there by two and two, so as to form perfect rings, which subsequently become isolated by the absorption of the interposed portion of the fibres. This development, he assures us, may be observed in an examination of the annular vessels in their earliest stage.

The solution of the question as to which of these two theories is the true one, will appear to many, in general, more simple and easy than it really is. It might be supposed that by means of a good microscope, used with the necessary skill and patience, the difficulties of research arising from the minuteness and softness of the vessels in their primary development would be easily surmounted. Such is in fact the case, though, nevertheless, this is not sufficient to place the matter in a clear light; for the principal difficulty in researches on the development of a vegetable organ arises, in the present as well as in most other cases, from the organ whose development is to be studied not presenting the same structure under all circumstances, but, on the contrary, presenting in the different cases subjected to examination greater or less deviations from the normal type. It is this circumstance which frequently hinders us from deciding whether we have a normal development before us, or only an accidental though persistent deviation. The observer, not seeing the successive development of an organ effected before his eyes, but having to establish his opinion on isolated facts observed at different stages of development, is often induced to consider some accidental and unimportant circumstance of greater interest than it really is, and thus founds upon these exceptions, although accurately observed, a theory entirely false. Only by researches frequently repeated can such errors be avoided.

Before passing to the examination of annular vessels, I shall offer some remarks on the fibre of spiral vessels.

Whoever has examined the development of spiral vessels and spiral cellules, and recognised their constant analogy with each other and with the dotted cellules, will not doubt for an instant that he sees in the fibre of spiral vessels, not a particular and independent organism, but rather the secondary membrane of the vascular utricles, divided in a spiral direction into one or more parallel bands. As regards the organization of this pretended fibre, I refer therefore to my work on the organization of the cellular membrane, because all that can be said on the structure of the membrane of the spiral cellule is equally applicable to the wall of the spiral vessel. But as respects what I have to say concerning annular vessels, it is necessary to examine with care some points relative to the spiral fibre.

In the memoir above quoted I have detailed their striæ, their great facility of tearing in a spiral direction, the hollows and furrows lying in a similar direction, and more especially the slits, which entirely penetrate the thickness of the cellular membrane, as the reasons which favour the opinion that the secondary cellular membranes possess a fibrous structure. All these phænomena, which are so frequently seen on the parts of the cellular membrane situated between the dottings on the cells, are also observable on the fibres of the unrollable spiral vessels; but are not so often recognised in the latter, either on account of the narrowness of the spiral fibre, or that frequently, even under the highest magnifying powers, the spiral fibre appears homogeneous. When, on the contrary, the fibre is of a considerable width, so that it rather resembles a flattened ribbon than a semi-rounded or quadrangular thread, it does not, in most instances, present a homogeneous aspect, but furrows more or less deep are observable in it in the direction of the fibre, either in one row or side by side, and in this last case they give to it a retiform appearance (Plate I. fig. 2. and 3, *Commelina tuberosa*). In other cases these furrows penetrate through the entire thickness of the fibre, which, at different points, is divided into two or more fibres placed side by side. These fibres either take a parallel direction, or the detached fibre at a greater or less distance reunites with the other, or else one of the fibres arising from division, leaving the other part, which continues in its primary direction, rises in a more oblique spiral direction, until it reaches the adjacent coil of the fibre into which it merges. Thus, in short, we observe, that almost all the modifications of form found in the secondary utricular layers result from the close union of all the constituent parts of the fibre, from their more or less de-

cided separation into isolated threads, from deviations in the course of these from that of the main-thread, or from a reticulated union of the isolated threads.

The direction in which the spiral fibre is wound has, indeed, no direct connexion with the organization of the vessel; nevertheless I think it necessary to make some remarks on this subject, because several erroneous statements, partly founded upon an imperfect knowledge of the spiral, have been advanced by some authors. I have elsewhere said that the great majority of spiral vessels were wound to the right; that is, the volution of the fibre is such, that, to an observer placed in the axis of the cylinder around which the spiral line rises, the fibre appears to mount from left to right, as shown in the vessel represented at figure 5. Like most other phytotomists, Schleiden says that the spiral fibre is wound sometimes to the right, sometimes to the left; and he thinks it possible to admit provisionally, as a general rule, that in spiral organizations "contemporaneously" developed, those which are situated immediately side by side in the direction of the radius have similar directions (*homodromes*), whilst those placed side by side in directions parallel to the periphery have different directions (*heterodromes*); and in proof of this law he relies on the constant crossing of the pore-like fissures in contiguous parenchymatous and ligneous cellules when observed in sections made parallel to the medullary rays. I must confess my inability to conceive how Dr. Schleiden can allege the crossing of the porous fissures in support of the volution of the fibres in different directions, since it proves quite the contrary. This crossing is seen when two vessels or cellules furnished with pores are superposed, and the adjacent parietes wound in opposite directions; but it is evident that this last case is only possible when the winding in the two vessels is homodromous*. It is quite true that we generally see the porous fissures crossing each other in a section parallel with the medullary rays; which proves that the different layers of cells visible in such a section and placed one under the other, are wound in a homodromous direction; but as at the same time the cells of every such layer are homodromous with each other, it clearly follows that, generally speaking, all the cells of a plant are homodromous; and this, in fact, will be found to be so on an examination of different sections of the same plant.

Without doubt spiral vessels exist which are wound to the left; but although I have latterly found them more frequently than formerly, I must still persist in asserting them

* [This illustration may be easily verified by applying two quills together, with equidistant homodromous or heterodromous spirals scratched upon them.—Ed.]

to be much rarer than those wound to the right, and that they should rather be considered as exceptions to the rule, since, in most plants, we find a hundred spiral vessels wound to the right for a single one wound to the left. Doubtless it is true that these proportions vary in different plants, and I cannot yet say whether the finding in them more frequently spiral vessels wound to the left be a fact peculiar to certain species or only to certain individuals: generally they are, as I have said, wound to the right. The volution to the right or to the left, in spiral vessels, is quite independent of the organization of the surrounding parts, as is proved by the fact that, in certain cases, not only the fibres of two superposed utricles of the same vessel are wound in opposite directions, but sometimes even in the same vascular utricle (as I have seen in the Gourd) the parts of the spiral fibre separated from each other by rings are wound in an opposite direction (Plate I. fig. 9).

When we examine the fibre of the perfectly developed annular vessel (for which researches I have been accustomed to use the *Commelina tuberosa*), we find its organization perfectly analogous to that of the spiral fibre, in the rings being composed sometimes of an apparently homogeneous substance, and sometimes exhibiting traces of a determinate structure.

In the broad fibres, as in the *Commelina tuberosa*, the fibre frequently exhibits a great number of shallow linear furrows or perfect fissures, forming a net-work of very narrow and elongated meshes (fig. 1, 3). More frequently still these fissures are found in an uninterrupted line in the medial line of the fibre, or they become confluent, and thus divide the ring into two superposed rings (fig. 4 *a, a*, *Commelina tuberosa*). When this latter division takes place, it generally recurs on every ring of a vessel. Frequently, however, this does not occur; but divided and undivided rings alternate in an irregular manner, the undivided rings being sometimes of equal size, sometimes of half the size of the divided rings, and sometimes of a size very inconsiderable in comparison with the divided rings (Plate I. fig. 1, *Commelina tuberosa*).

The direction of this line of division is parallel to the lateral edges of the ring, so that, by this fissure, the ring is divided into two superposed rings, which sometimes touch and sometimes are placed at a little distance from each other. According to Schleiden, this line of division proceeds from the coils of the spiral fibre being more or less completely soldered together, and always in pairs. We easily perceive that, in this case, the line of partition should be directed spirally from one edge of the ring towards the other, and that it should not be parallel

to its edges; but as the latter is constantly the case, we must reject this explanation of the origin of the line of partition.

In the developed annular vessel, the rings are either entirely isolated, or two or three are joined together in different ways. It not unfrequently happens that the line of partition does not divide the ring throughout the whole of its circumference, but that the two superposed rings are united for a space variable in extent; in which case the parts separated are removed to a greater or less distance from each other, and are placed obliquely to the axis of the vessel. (Plate I. fig. 6, *Commelina tuberosa*: the same form is often met with in the *Canna indica*.)

In other cases, and this is the habitual organization, the rings are removed to a greater or less distance from each other, and are separated by a regular spiral fibre, which, according to the distance of the rings, describes one or more volutions, and frequently even a great number. Of this there are several modifications: very generally from a ring will proceed a spiral fibre of the same width as the annular fibre, the distance of whose coils is nearly equal to that of the rings in the portion of the vessel which exhibits this structure (fig. 9, of the Gourd); the other extremity of the fibre being similarly annexed to a complete ring, followed by rings, either isolated or again reunited by spiral fibres.

Very frequently also the spiral fibre placed between two rings does not proceed to a junction with the rings, but its extremities become attenuated and terminate at some distance from the ring. In the stem of the Gourd this is nearly as frequent as the preceding case (fig. 2 a, *Commelina tuberosa*; fig. 9, Gourd).

Often also, from two diametrically opposite points of a ring proceed two fibres in a continuous parallel direction.

Cases are sometimes met with, although rarely, where two rings are united by fibres slenderer than the annular fibre, which generally form a single coil, or at least only a small number of coils (fig. 1, 7, 8, *Commelina tuberosa*). This occurs in a very evident manner in the vessels whose rings are not homogeneous, but where the spiral fibre is divided by several fissures into threads united in net-work, as in the vessel represented in figure 1. The width of the fibres uniting the different rings presents no exact proportion to the width of the annular fibre, being sometimes about the half of it (fig. 8), sometimes considerably less (fig. 1). The point of union of the spiral fibre with the annular fibre is especially deserving of consideration. When examined with a sufficient magnifying power, we sometimes find (fig. 7, 8) that a part of the annular fibre separates itself to ascend in a spiral di-

rection ; but that, in general, at the point of junction of the two fibres the annular fibre does not become thinner, the spiral fibre being attached only to the lateral edge of the annular fibre, which preserves an uniform thickness throughout its entire extent (fig. 1, 9, 10). There are even instances in which this union does not take place in the direction of the spiral, but where the spiral fibre terminates in two divergent branches (fig. 10 *a*, *Commelina tuberosa*) separating right and left, and confluent with the annular fibre.

An examination of the proportions above mentioned, between the annular fibres and the spiral fibres which unite them, must excite doubts of the accuracy of Schleiden's theory of the origin of annular vessels. In fact the division which takes place in many rings is, as we have seen, nothing less than a proof of the ring being composed of the two united fibres of a spiral fibre ; whilst, on the other hand, the direction of this division parallel to the edges of the rings is quite opposed to Schleiden's theory, and shows us that, in these more or less divided rings, we see a transition from the simple ring to two rings, situated at considerable distances from each other. An organization entirely analogous is also found in the spiral fibre, for there are spiral vessels traversed in the middle by a narrow fissure (fig. 4, 6, *Commelina tuberosa*), by which the decomposition of the simple spiral fibre into two fibres placed at certain parallel distances is indicated.

What chiefly militates against the formation of rings by the united spiral coils of a spiral vessel, is the proportion which the rings bear to the spirioid fibres which unite them. And first, when the organization of the vessels is very regular, the rings and the fibres are generally of the same width (fig. 4, 9), which could not be the case if the rings were composed of a double twist of the fibre. If then the spiral fibres which unite the rings are slender, the width of these fibres bears no exact proportion to the width of the rings and of the divisions perceived in them (fig. 1) ; moreover, the fibres are sometimes soldered to the rings, and sometimes separated from them. The spiral fibres, when they are united to the rings, cannot be considered in certain cases, and according to the form of the point of union, as a part of the fibrous mass which forms the ring, this part separating from the ring, and continuing in a spiral direction.

I have thought it right to explain these considerations, in the first instance, upon the annular vessels in a state of complete development, because observations made on developed vessels are necessarily more precise and certain than those made on young vessels ; not so much on account of the larger size of the developed vessels, but because, in consequence of

the greater thickness of their fibres, of the greater distance of these organs from each other, and of the absence of the mucilage with which the young vessels are gorged, these developed vessels present a much clearer contour, and the organization of their fibres is more easily observed. Doubtless it is true that we ought not to infer from the structure of a developed organ the mode of its development; but the examination of this structure is nevertheless of very great importance in studying the manner of its development, since we always thence obtain the means of proving the truth of any theory propounded on the history of development, a theory which ought not to be in contradiction with the results of an examination of the developed organ. Now in the present case this contradiction assuredly exists between the structure of the developed annular vessels and the theory of Schleiden.

Let us now see what information the examination of the young vessels gives us of the mode of their development. At first I selected the stems of different plants, especially of *Tradescantia tuberosa*, because Schleiden announced that he had remarked the metamorphosis of spiral vessels into annular vessels in the youngest internodes of subterranean and ascending stems. The results have not been favourable to the theory of Schleiden. For this examination it is not proper to select vessels placed at the interior angle of the vascular bundles, because these pass too rapidly through the phases of their development, and their diameter is also too small; the coils of their fibres being moreover at first too close together to allow any observations made upon them to be considered as conclusive. The larger vessels, placed more towards the exterior, present less difficulties in these respects, though here also an unfavourable circumstance occurs, viz. that the rings in the course of their development, in consequence of the feeble longitudinal growth of the vascular utricles, remain very close together, which may, in some cases, render the distinction of the annular and spiral formations in the fibres difficult, and which, in all cases, makes it rather hard to decide whether there does or does not exist between each pair of rings a slender spiral fibre which is subsequently absorbed. However I think I have observed with certainty, that from the beginning, and so soon as I could distinguish the fibres on the interior surface of the vascular utricle, under the form of thin, more or less narrow, diaphanous edges, they were not absolutely spiral; but that, as in the developed vessels, they formed either complete isolated rings, or rings intermixed with spiral fibres; so that, with the exception of the thinness of the fibres, and of the small distance of the rings from each other, there

is no essential difference observable between them and the perfectly developed vessels.

The examination of the vessels of the stem not having, however, furnished me with a perfectly satisfactory result, and my former researches on the roots of Palms and other monocotyledonous plants having shown me the greater facility of studying the development in this organ than in the trunk, I submitted the roots of *Tradescantia* to a very attentive examination, the results of which I consider to be quite conclusive. The examination of the roots presents this great advantage over that of the stems, that in the larger vessels, placed nearer to the centre, the fibres are not developed until a sufficiently late period, when their longitudinal growth is already terminated. At the period when the fibres of the vascular utricles are developed, these utricles have not only already attained to a considerable size, but the fibres in them are also, from the beginning, arranged at greater distances from each other, and their successive development may be followed in detail step by step, from one end of the root to the other. This examination is rendered easier in consequence of the vessels being deposited in a very transparent cellular tissue. In these researches I have recognised with the greatest clearness, and with a perfect conformity to what I had previously observed in the roots of Palms, that, from the time when the fibres make their appearance, and when they are still so tender, narrow and transparent, that it is often only possible to see them with a faint light, they already present all the different modifications of form which are observed in the perfect vessels. We then find, as at a later period, the same alternation of annular and spiral and reticulated fibres; but I have never seen the least trace of the formation in all vascular utricles of a spiral fibre whose coils would unite in pairs, and the portions of the spiral fibre serving as the means of union be absorbed; and I consider it as perfectly impossible that this transition of spiral vessels into annular vessels, if it existed, could have escaped me, because in a great number of roots I have followed the vessels from the moment when the utricles presented closed cells with thin parietes, and enclosed a nucleus.

Hence it results that the development of the annular vessels agrees with the observations made on the perfect vessels. Researches into these two organs show that annular, spiral, and reticulated vessels afford three different forms, very intimately connected, and passing frequently one into the other; but that they must not be considered as temporary degrees of metamorphosis of the same vascular utricle. It is true that

